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Coordination in prehension

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Abstract Prehension involves the coordination of a reaching and a grasping movement, such that the hand opens and closes in tune with the transport of the hand to the object to be grasped. To investigate this coordination, we focused on the transition from hand opening to hand closing in the grasping component of prehension. Earlier research has suggested that the time taken to close the hand remains constant over varying reaching amplitudes. In the present experiment, in which subjects reached for objects at six different distances and for objects that moved away from them at three different, constant speeds, hand-closure time was found to vary as a function of experimental conditions. Moreover, initiation of hand closure did not occur at a constant value of the (perceptually available) first-order time remaining until contact with the object. However, the variations observed, occurring as a function of initial hand-object distance and object speed, could be accounted for by an abstract dynamical model of perceptually driven postural changes.

Key words Human · Movement · Prehension

Introduction

A prehensile act requires coordination of its two constituent components, the transport or reach component, bringing the hand into the vicinity of the object to be grasped, and the grasp component, ensuring that the object be enclosed. Natural prehension is characterized by the hand opening and closing in tune with the movement of the hand toward the target object. Accordingly, prehension involves the control of both its reach and its grasp components, as well as their coordination. Since the seminal work of Jeannerod (1981, 1984, 1986) and Arbib (1981, 1985), the issue of how such coordination is achieved has been a subject of debate and has inspired a consequential number of experimental investigations on the nature of the coupling of the two components.

According to Jeannerod (1981, 1984) and Arbib (1981, 1985), the reach and grasp components evolve independently and are coordinated through a (hierarchically higher) central timing mechanism. This timing mechanism ensures the temporal alignment of key moments in the evolution of the two components: for instance, Jeannerod (1981, 1984) suggested that the central timing mechanism operates such that peak hand aperture – a characteristic of the grasp component – is reached at the moment of onset of the "low-velocity phase" of the reaching movement (i.e., at the moment of peak deceleration of the latter). A number of experiments in which object size, orientation, and/or distance (Gentilucci et al. 1991; Jakobson and Goodale 1991; Marteniuk et al. 1990; Paulignan et al. 1991b; Wallace et al. 1990) were systematically varied, however, failed to provide evidence for the postulated coincidence of these or other "key moments." In search of other characteristics of the coupling that might then reveal the operation of a central timing mechanism responsible for the control of coordination, Gentilucci et al. (1992) noted that the duration of hand closure remained constant over a range of reaching amplitudes. This invariance was found, moreover, to be maintained over conditions in which object location was changed immediately after movement initiation. This led Gentilucci et al. (1992) to suggest that the initiation of hand closure (grasp component) was timed on the basis of the time remaining before the hand reached the object (reach component).

The notion of a temporal coordination between reaching and grasping that involved keeping constant

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the duration of hand closure was included in Hoff and Arbib's update (1993) of Arbib's original (1981) model.[1] The coordination mechanism in the model is based on prior knowledge of the duration of hand closing. Hoff and Arbib (1993) argued that when the time required for opening the hand, the time required for closing the hand, and the time required to transport the hand to the object are all known, the estimated movement time will be either the time needed for hand opening plus closing or, if longer, the time needed for hand transport. In the latter case, the opening of the hand is prolonged in order to keep the duration of hand closing fixed. If, on the other hand, hand opening and closing times determine overall movement duration, the duration of the transport component is lengthened accordingly. Importantly, Hoff and Arbib did not suggest that closing times should be equal for movements performed under different conditions (e.g., reaches to grasp differently sized spherical objects yield different closing times; see Von Hofsten and Rönnqvist 1988).[2] The model states that, within a specific movement, closing time is a controlled variable, in the sense that it is stable against perturbations (Schöner 1995).

Rather than focusing on the *temporal* coupling of reaching and grasping, Haggard and Wing (1991, 1995) note that *spatial* relations between these two components are highly stable. They studied the traces of normal and perturbed prehensile movements in a state space with hand position and hand aperture size as dimensions. Unperturbed movements exhibited typical traces in this space. Haggard and Wing (1991, 1995) showed that, after mechanical perturbation of the reaching arm, trajectories in state space returned to these traces, implying that the spatial relation between hand position and hand aperture size is stabilized by the system. This is consistent with recent findings with respect to altered initial hand configurations. If people start out their reaches with an open-hand configuration instead of a more-often-studied closed-hand configuration, their hand aperture size decreases initially toward the appropriate trajectory, as observed in the condition in which the hand was initially closed (Saling et al. 1996; Timmann et al. 1996).

Coupling of reaching and grasping on the basis of time to contact

In Hoff and Arbib's (1993) model, an estimate of the time required to close the hand (MT_{close}) is used as an input variable. On the basis of knowledge of the total movement duration (MT_{tot}, another input variable), monitoring the unfolding of the reaching movement allows starting hand closure at the designated time (i.e., at $MT_{tot}-MT_{close}$). Control in such a scheme assumes that the ordering of events is accomplished by time-keeping from the start of the movement onward. An alternative way of timing hand closure might be based on time-keeping with respect to the endpoint of the movement, as would result from using time-to-contact rather than time-from-initiation information (Bootsma and van Wieringen 1992). Whereas monitoring time from initiation is achieved by reliance on internal time-keeping procedures, time-to-contact information can be obtained visually, as was first demonstrated by Lee (1976) and recently generalized to include all types of rectilinear approach by Bootsma and Oudejans (1993). It is important to note that the temporal optical variable proposed in fact specifies the time remaining until contact if the velocity of approach were to remain constant; that is, it specifies the first-order[3] temporal relation $TC_1(D)=-D/\dot{D}$ where D is the current distance and $-\dot{D}$ the current approach velocity (i.e., the rate of change of D, negative because the distance decreases). In the case of reaching for an object while assuming a straight trajectory of the hand toward the target – an assumption justified by the observation that trajectories of goal-directed movements normally deviate from a straight line only slightly; see Morasso (1981) and Haggard and Richardson (1996) – information concerning time to contact between the hand and the object (see Fig. 1) is contained in the combination of the relative rates of change of the optical angles subtended by the hand (i.e., φ) and by the gap (i.e., θ) separating hand and object (for a discussion on the use of this variable in different situations, see Bootsma and Oudejans 1993; Bootsma and Peper 1992):

$$\frac{1}{TC_1(D)}=-\frac{\dot{D}}{D}=-\frac{\dot{H}}{H}-\frac{\dot{\theta}}{\tan\theta}=\frac{\dot{\varphi}}{\sin\varphi}-\frac{\dot{\theta}}{\tan\theta}=\frac{1}{\tau(\varphi,\theta)} \quad (1)$$

While reaching to pick up an object, both the optical angle subtended by the hand (i.e., φ) and the optical angle subtended by the gap separating the hand from the object (i.e., θ) decrease. As demonstrated by Eq. 1, in such a sit-

[1] In addition to a modification of the coordination mechanism of reaching and grasping, Hoff and Arbib (1993) also proposed new control structures for trajectory formation in both components, as well as an abandoning of the division of the movement into a ballistic portion and a portion under feedback control. For the present discussion, we focus on the coordination mechanisms introduced in their model.

[2] In general, the literature shows that closing times decrease with increasing object diameter [explicitly tested by Von Hofsten and Rönnqvist (1988), but also apparent in the results of Berthier et al. (1996) and Marteniuk et al. (1990)]. In the case of nonspherical objects, however, no relation between object size and hand-closure time is apparent in the existing literature (Jakobson and Goodale 1991; Zaal and Bootsma 1993). This difference in results can be attributed to the fact that, for spherical objects, size and available contact area are confounded (Bootsma et al. 1994; Zaal and Bootsma 1993).

[3] In order to avoid confusing the specificational (i.e., optic) variable and the temporal relation that it specifies, Bootsma et al. (1997) suggested labeling the specificational (optic) variable $\tau(I)$, where I stands for the informational flow quantity [e.g., the relevant optic angle(s)], and labeling the first-order temporal relation specified TC_1(EAS), where EAS stands for the environment-actor system property of interest (e.g., distance D in Fig. 1). The subscript '1' indicates the first-order nature of the temporal relation between observer and object (i.e., taking into account only the first-order time derivative $\dot{D}$). In the case of a second-order relation (taking into account $\ddot{D}$), the symbol TC_2 would be used.

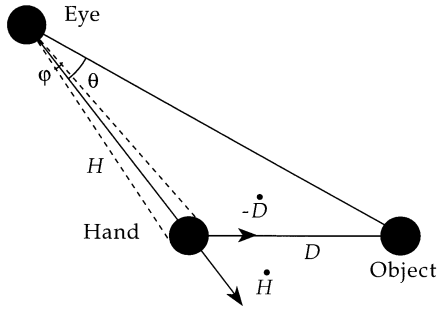

Fig. 1 Schematic representation of the momentary relations between eye, hand, and object (φ optical angle subtended by the hand, θ optical angle subtended by the gap separating hand and object, D current distance between hand and object, $\dot{D}$ rate of change of D, H current distance between eye and hand, $\dot{H}$ rate of change of H)

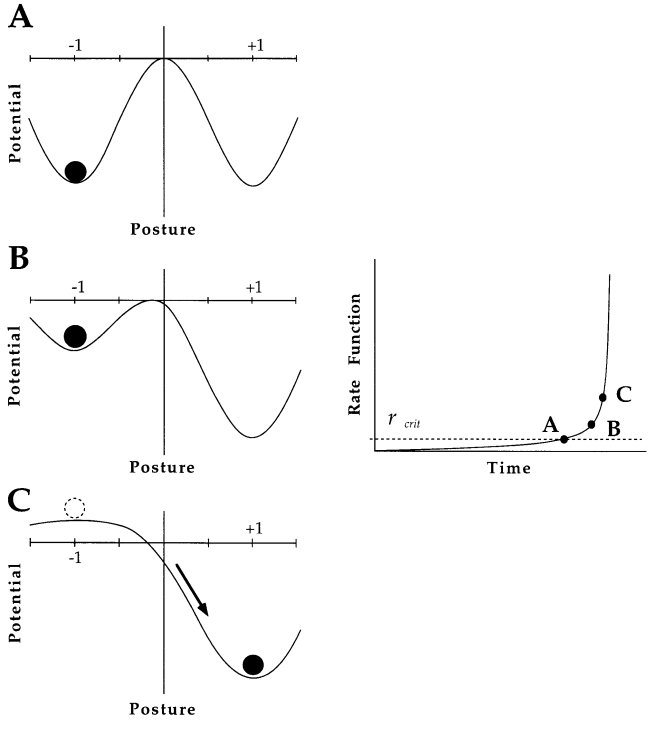

Fig. 2A–D Schematic representation of Schöner's (1994) model of dynamical perception-movement coupling. Under influence of the rate function (**D**), the attraction of the potential well that is associated with an initial posture (x=–1) decreases and the attraction of the potential well associated with a final posture (x=+1) increases. At the moment the former well vanishes, a posture change occurs (r_{crit} critical value of rate function)

uation the optical variable $\tau(\varphi, \theta)$ specifies the first-order temporal relation $TC_1(D)$.

The use of time-to-contact information

If indeed timing of hand closure in prehensile acts is achieved on the basis of such time-to-contact information, two mechanisms for the way it may be used to accomplish the coordination of reaching and grasping can be distinguished.

First, the initiation of hand closure might be triggered by a specific threshold value of the optical variable τ. Threshold values of τ have indeed been reported, for instance with reference to the initiation of wing folding for diving gannets (Lee and Reddish 1981). However, close analysis of the experimental evidence provided has raised serious doubts with respect to the pertinence of the empirical support invoked in support of this hypothesis (cf., Wann 1996), while Bootsma et al. (1997) have recently questioned the theoretical rationale underlying the τ-threshold hypothesis, emphasizing the distinction it creates between the control of movement initiation and the control of movement execution.

Second, movement might be continuously geared to τ (Bootsma et al. 1997; Lee and Young 1985; Lee et al. 1983; Savelsbergh et al. 1991). Of particular interest for the present purposes is Schöner's (1994) dynamical model in which such gearing emerges from a continuous dynamical coupling between perceptual information and movement. This model addresses the switching from one posture to another posture. As an example, Schöner (1994) refers to the aforementioned gannets folding their wings. In the model, both the unfolded-wings posture and the folded-wings posture are represented by point attractors in an abstract dynamical landscape. These attractors can be visualized[4] as two wells in a potential field, as sketched in Fig. 2. Along the horizontal axis, the possible postures are represented by the numbers –1, associated with an open-wings posture, and +1, associated with a closed-wings posture. The ball represents the current posture, which at the start of the gannet's dive is a stable open-wings posture.

During the dive, time-to-contact information is generated. In Schöner's model, the inverse of the τ-variable (which we will call the rate[5] function $r(t)=\tau^{-1}$) affects the stability of the two attractors. If $r(t)$ is smaller than a critical value r_{crit}, the potential well that is associated with the unfolded-wings posture becomes deeper, while

[4] We would like to explicitly point out that our graphical representation of the model presented by Schöner (1994) exclusively aims at explaining the basic mechanisms. For this purpose, we translated the basic features of the model into a description of a potential field. In contrast with, for instance, the potential field describing the dynamics of phase transitions in the finger-wiggling experiments of Kelso and colleagues (Haken et al. 1985), where the shape of the potential field is directly related to the model equations, the illustrations presented here only serve to communicate the mechanism involving a change in posture.

[5] In contrast to the examples modeled by Schöner (1994), in which relevant structures in the optic array expand, relevant optical structures contract in the case of reaching to pick up an object. Since Schöner (1994) labeled the relative rate of optical expansion $e(t)$, we therefore might have labeled the relative rate of optical contraction $c(t)$. In order to emphasize that the model is valid in both the situation of optical expansion and optical contraction, dependent in both cases on the evolution of its relative rate of change, we chose to label the function associated with the influence of optical information on the intrinsic dynamics $r(t)$ or, as a function of the distance D, $r(D)$. The symbol 'r' refers to the relative *rate* of optical change (expansion or contraction).

the potential well associated with the folded-wings posture becomes shallower. The opposite holds if $r(t)$ is larger than r_{crit}. During the dive of the gannet, the magnitude of $r(t)=\tau^{-1}$ increases (because τ itself decreases toward zero). Figure 2B and C illustrates the effects on the depth of the potential wells related to this increase in $r(t)$. The transition from the unfolded-wings posture to the folded-wings posture occurs as a consequence of the change in the relative stability of the two corresponding attractor states. In Fig. 2C, the ball has rolled into the potential well that is associated with the folded-wings posture that has become the only stable state. An additional feature of the model, viz. the postulated limit-cycle properties of the dynamical system, ensures the stability of the transition trajectory. In this model, the transition from one posture into another posture is thus guided by a *continuous* coupling of the posture dynamics with optical information. This mechanism allows for flexible behavior in the case of changing circumstances (perturbations) such as changes in the level of the water surface or disturbances by the wind in the case of the diving gannets (Schöner 1994).

By adopting this model for describing coordination in prehension, a continuous informational coupling is suggested to be involved in the coordination of the reach and grasp components. Accordingly, the transition from a hand-opening regime to a hand-closing regime will be due to a change in stability of fixed points under the influence of optical information $[r(t)=\tau^{-1}]$ generated by the reach component (i.e., by the movement of the hand toward the object). Note that Schöner's (1994) model is an abstract mathematical model that captures the timing of the change of regimes, while ignoring their detailed kinematics. We adopted this model to investigate the timing of the initiation of hand closing in the grasp component of prehensile movements.

The present study

The above considerations were the starting points for the present study. First, the suggestion of Gentilucci et al. (1992) that hand closing time (HCT) is kept constant will be evaluated by systematically varying reaching amplitude. Second, the possibility of a constant τ-threshold value at the moment of initiation of hand closure will be considered. Finally, the possible coordination of reaching and grasping on the basis of a dynamical coupling via this source of information will be explored. The latter two mechanisms are mutually exclusive, since Schöner's (1994) dynamical model predicts that differences in the reaching kinematics give rise to different τ-values at the moment of hand closure initiation. Both mechanisms, however, might lead to constant closure times, which remains to be evaluated. Importantly, the τ-based models state that the details of the kinematics of the reach component determine the evolution of the τ-values over time, and thus the timing of the grasp component.

A data set with respect to prehension, which was earlier analyzed in order to investigate the dynamics of the reach component[6] (Zaal 1995; Zaal et al. 1998) was reanalyzed for the present purposes. Below, only a brief description of the experimental conditions is provided. For more a detailed description the reader is referred to Zaal 1995 or Zaal et al. 1998.

Materials and methods

Four men and six women (20–31 years of age) were required to reach for and grasp a cylindrical wooden disk, with a diameter of 5 cm and a height of 2.5 cm, which was placed on the arm of a drafting plotter (Roland DG DPX-2200). The object could be located at a distance of either 20, 25, 30, 35, 40, or 45 cm from the initial hand position in the sagittal plane. In three other conditions, the plotter arm, and thus the object, moved away from the subject (in the sagittal plane) at one of three constant velocities (25, 35, or 45 cm/s). In the latter conditions, the object started at 20 cm from the initial hand position. Subjects were instructed to wait for a "go" signal (a tone presented by a pair of headphones) and subsequently pick up the object between the index finger and thumb as accurately and as quickly as possible. In the moving-objects conditions, this go signal was presented 100 ms after the object had started moving, when the object had reached a constant speed. In the six stationary-object conditions, as well as in the three moving-object conditions, data were collected using a two-camera Selspot system, recording the positions of infrared light emitting diodes (IREDs) attached to the subject's index finger and thumb, as well as to the object. Each condition was presented ten times in a randomized order. After removing high-frequency noise from the recorded data (using a recursive second-order Butterworth filter at a cut-off frequency of 8 Hz), three-dimensional real-world coordinates were obtained by means of the direct linear transformation (DLT) method (Abdel-Aziz and Karara 1971). Hand aperture (describing the evolution of the grasp component) was defined as the distance between the IREDs on the thumb and the index finger, while hand position (describing the evolution of the reach component) was defined as the location of the midpoint of these two IREDs along the axis connecting initial hand position and target object position. Movement onset was defined as the moment that hand velocity reached a value of 5 cm/s. The moment that grip-closing velocity fell below 7.5 cm/s was taken as the moment of movement termination. These velocity criteria were chosen so as to be applicable to all trials under all conditions.

Results and discussion

Figure 3 shows examples of time courses of hand aperture in the nine experimental conditions, all from the same participant. HCT was defined as the time from peak aperture until grasp movement termination. Table 1 presents the values of HCT averaged over subjects.

Gentilucci et al. (1992) suggested that HCT would be kept constant and would thus be independent of reaching amplitude (in the stationary object conditions) and of object speed (in the moving object conditions). A repeated-measures ANOVA on HCT in the stationary-object condi-

[6] The analyses carried out with respect to the reach component focused on a comprehensive model for the variations in reach kinematics, and more specifically the relations among movement amplitude, movement speed, and movement duration. The dynamical model derived in that study will be used here to model the kinematics of the reaches. On the basis of these kinematics, continuous time courses of τ-values will be computed, which will then be entered in the model of a continuous dynamical coupling of reaching and grasping, which is the focus of the present contribution.

Table 1

		Stationary objects (cm)						Moving objects (cm/s)		
		20	25	30	35	40	45	25	35	45
HCT (ms)	*M*	121.7	121.7	130.6	144.4	147.5	145.6	140.7	142.2	153.5
	SD	12.3	13.8	21.0	23.0	20.7	21.7	17.7	17.4	25.6
$TC_1(D)$ (ms)	*M*	47.1	40.1	44.4	46.5	50.6	50.6	39.5	45.6	50.1
	SD	10.4	10.4	11.8	13.4	13.7	15.2	9.8	11.8	14.2

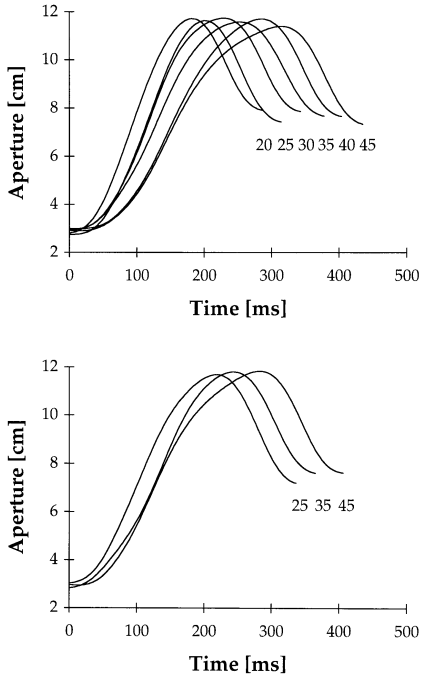

Fig. 3 Examples, all from the same subject, of aperture profiles of movements toward stationary objects at six different positions (*upper panel*) and toward objects moving at three different velocities (*lower panel*). Labels indicate movement amplitude (*upper panel*) and object speed (*lower panel*), respectively

tions, however, revealed a significant effect of movement amplitude ($F_{5,45}$=13.44, P<0.001). Trend analysis showed a linear increase in HCT with increasing amplitude ($F_{1,9}$=61.66, P<0.001), whereas nonlinear trends were not significant. In the moving-object conditions, the effect of object speed did not reach significance, although a tendency toward an increase in HCT with increasing object speed could be observed ($F_{2,18}$=3.41, P=0.056). The present results, which are based on a relatively large data set, are thus in contradiction with Gentilucci et al.'s (1992) suggestion.

The second point to be addressed concerned the prediction of the constant τ-threshold hypothesis that hand closure would be initiated at a constant value of the optical variable τ. In order to examine this prediction, the values of the first-order time-to-contact variable $TC_1(D)$ – being the EAS variable specified by τ (see footnote 3) – at the moment of onset of hand closure were calculated by dividing remaining distance between hand and object at the moment of peak aperture by the hand velocity relative to the object (Eq. 1); mean values are presented in Table 1 (see also Fig. 6). For the stationary-object conditions, a repeated-measures ANOVA showed a significant reaching amplitude effect ($F_{5,45}$=4.30, P<0.005). As can be seen from Table 1, $TC_1(D)$-values increased with increasing reaching amplitude for all but the smallest movement amplitude. Indeed, a trend analysis showed both a significant linear trend ($F_{1,9}$=5.13, P<0.005) and a significant nonlinear trend ($F_{4,36}$=3.75, P<0.005). In the moving-object conditions, object speed also had a significant effect on the $TC_1(D)$-values ($F_{2,18}$=10.47, P<0.005). A significant linear trend ($F_{1,9}$=18.04, P<0.005) was associated with this main object-speed effect. Inspection of Table 1 shows that the $TC_1(D)$-values in the moving-object conditions were of the same order of magnitude as those in the stationary-object conditions.

Thus we conclude that neither was the duration of hand closure kept constant nor was hand closure initiated at a constant value of the perceptually available first-order time to contact.

Continuous information-based coupling

Our short introduction of Schöner's (1994) mathematical model of the dynamics of perception-action systems aimed at communicating its basic mechanism. We will now specify the model equations for prehension[7] and then determine whether their numerical simulations capture the actual data concerning the moment of hand-closure initiation.

In the model, the grasping state is represented by a dynamical variable (x) with values ranging between –1 and +1. The extreme values represent a hand-opening regime (x=–1) and a hand-closing regime (x=+1). The change of this variable over time (i.e., $\dot{x}$) is determined by both its intrinsic dynamics (f_{grasp}) and the vision dynamics (f_{vision}) that are coupled to the intrinsic dynamics:

$$\frac{d}{dt}\begin{pmatrix} x \\ \dot{x} \end{pmatrix} = f_{\text{grasp}} + f_{\text{vision}}. \qquad (2)$$

The intrinsic dynamics include the two fixed points, representing the stable initial and final states, and the limit cycle that stabilizes the transient trajectory. Accordingly, the intrinsic dynamics are modeled such that stable

[7] Although the model equations are straightforward translations of the equations presented by Schöner (1994), we preferred to provide them here (a) for reasons of conceptual clarity and (b) in order to correct minor errors that had crept into Schöner's equations.

fixed points exist at the values x=–1 and x=+1 (f_{open} and f_{close}, respectively), with a limit cycle passing through these points (f_{osc}). The proposed mathematical model showing these properties follows (cf. Schöner 1994):

$$f_{grasp} = f_{osc} + f_{open} + f_{close} \tag{3a}$$

in which

$$f_{osc}(x, \dot{x}) = \begin{pmatrix} \alpha & \omega \\ -\omega & \alpha \end{pmatrix} \begin{pmatrix} x \\ \dot{x} \end{pmatrix} - \gamma \begin{pmatrix} (x^2 + \dot{x}^2)x \\ (x^2 + \dot{x}^2)\dot{x} \end{pmatrix} \tag{3b}$$

$$f_{open} = -\beta_{int} f_{range}(x, \dot{x}, x_{open}, \dot{x}_{open}) \begin{pmatrix} x - x_{open} \\ \dot{x} - \dot{x}_{open} \end{pmatrix} \tag{3c}$$

$$f_{close} = -\beta_{int} f_{range}(x, \dot{x}, x_{close}, \dot{x}_{close}) \begin{pmatrix} x - x_{close} \\ \dot{x} - \dot{x}_{close} \end{pmatrix} \tag{3d}$$

and

$$f_{range}(x, \dot{x}, x_i, \dot{x}_i) = \exp\left[-\frac{(x - x_i)^2 + (\dot{x} - \dot{x}_i)^2}{2\sigma^2} \right] \tag{3e}$$

In our graphical illustration of the model (Fig. 2), the intrinsic dynamics constant β_{int} and the function f_{range} in Eq. 3c–e would determine the depth and the shape of the two potential wells, associated with the hand-opening and hand-closing regime, respectively. The constant σ is related to the width of the basin of attraction. The intrinsic grasp dynamics defined above are coupled to the vision dynamics through the inverse τ-function of the optical angles subtended by the hand and the gap separating the hand and object. Therefore, we defined the rate function $r(D)=\tau(\varphi,\theta)^{-1}$ as the inverse of $TC_1(D)$. The mathematical formulation of the vision dynamics is given by:

$$f_{vision} = \beta_{vision}(D) \left[+f_{range}(x, \dot{x}, x_{open}, \dot{x}_{open}) \begin{pmatrix} x - x_{open} \\ \dot{x} - \dot{x}_{open} \end{pmatrix} - f_{range}(x, \dot{x}, x_{close}, \dot{x}_{close}) \begin{pmatrix} x - x_{close} \\ \dot{x} - \dot{x}_{close} \end{pmatrix} \right] \tag{4a}$$

where

$$\beta_{vision}(D) = c_{vision}(r(D) - r_{crit}) \tag{4b}$$

with $\beta_{vision}(D)$ defining the degree to which the intrinsic dynamics are influenced by the vision dynamics. Gain constant c_{vision} and threshold r_{crit} determine the extent and the sign (weakening or strengthening of the attraction) of the influence, respectively. One might note the similarity of the functions associated with the fixed points (Eq. 3c, d) and the righthand side of Eq. 4a, representing the influence of the optical information on the stability of these fixed points. The (changing) effect of $\beta_{vision}(D)$ in Eq. 4a is equivalent to the effect of the constant β_{int} in Eq. 3c, d. Since $r(D)=\tau^{-1}$ increases during the movement, the potential well representing the hand-opening regime will vanish (because the signs of the contribution to this well in Eqs. 3c and 4a are different), whereas the attraction of the fixed point representing the closed-hand configuration will be strengthened (because of the equal signs in Eqs. 3d and 4a).

To evaluate model predictions, hand velocity relative to the object $\dot{D}$ and remaining distance between hand and object D must be known, both as a function of time, in order to determine the evolution of $r(D)=\tau^{-1}$ (which, we recall, is equivalent to $\dot{D}/D$; see Fig. 1). Zaal et al. (1998; see also Zaal 1995) demonstrated, on the basis of an analysis of the characteristics of the reach component of the present data set, that the dynamics of the latter are captured, over a large part of the movement, by the following equation of motion (with hand position D, velocity $\dot{D}$, and acceleration $\ddot{D}$:

$$\ddot{D} + \omega_R^2 D + \alpha_R D^3 + \beta_R \dot{D} + \gamma_R \dot{D}^3 = 0 \tag{5}$$

in which ω_R^2, α_R, β_R are constants and γ_R varies with amplitude. To distinguish the reach dynamics from the grasp dynamics, we added the subscript 'R' to the parameters associated with the reach component in Eq. 5. Kinematics obtained from numerically simulating this model were used to arrive at representative time courses of rate functions $r(D)$ for each condition.

Figures 4 and 5 present the results of nine numerical simulations representing reaches toward the six stationary objects and reaches toward three moving objects, respectively. The upper panels depict the rate function $r(D)=\tau^{-1}$ as a function of time, obtained by simulations of the dynamics of the reaching movement (Eq. 5). The lower panels depict the results of numerical simulations of the grasp dynamics (Eqs. 2–4) under the influence of the rate functions thus obtained.[8] For these simulations, the gain constant c_{vision} (Eq. 4b) was set at a value such that the $TC_1(D)$-values obtained from the simulations were on the same order of magnitude as the experimentally observed $TC_1(D)$-values. All other parameters in the model (Eqs. 3b–e) were given the same value as in Schöner's (1994) model describing the wing folding of the diving gannets. No attempts were made to optimize the fit of the model.

As a result of the loss of stability of the fixed point associated with the hand-opening regime (x=–1), the state variable travels to the fixed point associated with the hand-closing regime (x=+1). In accordance with the procedure adopted by Schöner (1994), the moment that this variable passed zero was taken to indicate the moment of initiation of hand closure. In order to compare the simulated data with the experimentally obtained data,

[8] The time courses of the rate functions depicted in Figs. 4 and 5 are based on numerical simulations of Eq. 5 in which only the value of γ_R was varied as a function of initial hand-object distance, with parameter values adopted from Zaal et al. (1998; Zaal 1995). Because these values were derived from mean kinematic patterns, the times of occurrence of the zero-crossings of the state variable x are representative of the mean patterns. In order to model individual trials, such as those presented in Fig. 3, trial-by-trial parameterization of the equation of motion of the reaching component (i.e., Eq. 5) would be needed.

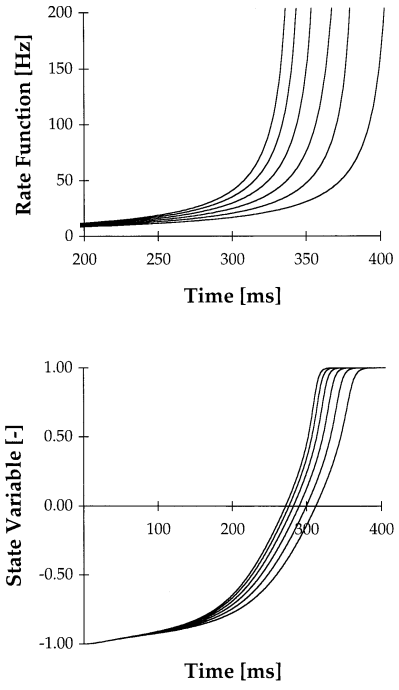

Fig. 4 Rate functions (*upper panel*) and time courses of hand configuration x (*lower panel*) in the six stationary object conditions, obtained by numerical simulations (see text for details). Simulation parameters for the grasp component: $\alpha=\omega=\gamma=10\,\mathrm{Hz}$; $\beta_{int}=40\,\mathrm{Hz}$; $\sigma=0.5$; $x_0=-1$; $c_{vision}=2.6$; and $r_{crit}=0$ Hz. Simulation parameters for the reach component: $\omega_R^2=92.8\,\mathrm{s}^{-2}$; $\alpha_R=-0.00789\,\mathrm{cm}^{-2}\,\mathrm{s}^{-2}$; $\beta_R=-6.0\,\mathrm{s}^{-1}$; and $\gamma_R=9.71\times10^{-4}$, 6.41×10^{-4}, 4.63×10^{-4}, 3.57×10^{-4}, 2.89×10^{-4}, and 2.45×10^{-4} $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$ for the conditions with reaching amplitudes of 20, 25, 30, 35, 40, and 45 cm, respectively.

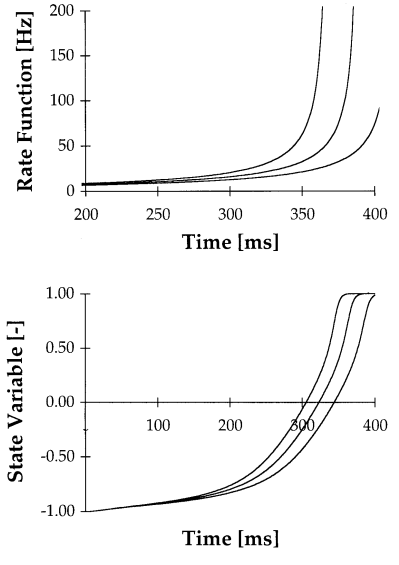

Fig. 5 Rate functions (*upper panel*) and time courses of hand configuration x (*lower panel*) in the three moving object conditions, obtained by numerical simulations (see text for details). Simulation parameters for the grasp component: $\alpha=\omega=\gamma=10\,\mathrm{Hz}$; $\beta_{int}=40\,\mathrm{Hz}$; $\sigma=0.5$; $x_0=-1$; $c_{vision}=2.6$; and $r_{crit}=0$ Hz. Simulation parameters for the reach component: $\omega_R^2=92.8\,\mathrm{s}^{-2}$; $\alpha_R=-0.00789\,\mathrm{cm}^{-2}\,\mathrm{s}^{-2}$; $\beta_R=-6.0\,\mathrm{s}^{-1}$; and $\gamma_R=9.71\times10^{-4}\,\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$

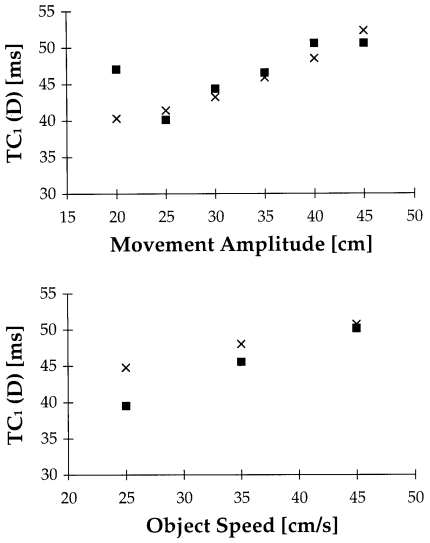

Fig. 6 Experimentally (*squares*) and numerically (*crosses*) obtained first-order hand-object time to contact values [$TC_1(D)$] at the moment of onset of hand closure under the stationary-object conditions (*upper panel*) and under the moving-object conditions (*lower panel*)

$TC_1(D)$-values were computed (from the dynamical model of the reach component as described in Eq. 5) at the moment that $x(t)$ became positive. Figure 6 depicts the $TC_1(D)$-values obtained experimentally and by simulation, for the stationary-object conditions (upper panel) and for the moving-object conditions (lower panel), respectively. Given that, apart from the gain constant c_{vision}, none of the other parameters of Schöner's (1994) model for wing closing in diving gannets were adapted, the resemblance between the experimental and simulated data (except for the 20-cm stationary-object condition) was found to be quite satisfactory.

Conclusion

Gentilucci et al.'s (1992) suggestion that HCT would be kept constant in prehension led Hoff and Arbib (1993) to postulate a coordination mechanism based on prior knowledge of the duration of hand closure. Based on a relatively large data-base, the results of the present study indicated that, contrary to Gentilucci et al.'s suggestion, HCT increased with increasing reaching amplitude. Such a result, however, does not necessarily invalidate Hoff and Arbib's model, because it does not, strictly speaking, require a fixed duration of hand closure: The crucial assumption of their model is that the duration of closure time is known prior to the movement. Nevertheless, the fact that this duration varies as a function of movement amplitude (and perhaps object speed) implies that the influence of the latter variable(s) would have to be accounted for by a structure dedicated to the estimation of HCT, once more increasing the already important number of input variables associated with this model.

An alternative to timing the initiation of hand closure on the basis of advance knowledge of HCT would be its timing on the basis of information about the time remaining until hand-object contact is established. This latter type of information is generated during the movement and can, thus, be used "on the fly." Previous research on the use of a similar optical variable in birds and humans suggested that also, in situations where acceleration is present, timing may be based on this kind of first-order temporal information (Lee and Reddish 1981; Lee et al. 1983). As argued in the Introduction, two different ways in which such predictive information may be used can be distinguished. On the one hand, it has been proposed that movement (in this case, hand closure) initiation results from the crossing of a threshold value of the relevant information source. In line with the recent literature (Wann 1996), such a τ-threshold hypothesis is not supported, as our results indicate that $TC_1(D)$-values at the moment of hand closure initiation were not constant over different conditions. The possibility of a continuous dynamical coupling of reaching and grasping through optical information, on the other hand, allowed for variations in both closure durations and the values of the time-to-contact variable at the moment of hand-closure initiation. In such a continuous dynamical perception-movement coupling perspective, movement of the hand toward the object to be grasped (reach component) creates the information that is subsequently used in the timing of the grasp component, thus eliminating the need for a control-of-coordination structure. Different reaching amplitudes (and object speeds) give rise to differences in the kinematics of the reaching component and, hence, differences in the evolution of the temporal information generated by the approach of the hand toward the object. As the grasp component is geared to this information, the timing of the grasp component will reflect these differences.

Importantly, the proposed model relates to the studied movement at its timing level and not to its detailed kinematics (Schöner 1995). As such it can be regarded as a next step in the process of modeling the complete reach-and-grasp dynamics (cf. Zaal 1995; for a similar approach with respect to the dynamics of reaching, see Schöner 1990; Zaal et al. 1998). A comprehensive model of coordinated reaching and grasping, however, should include a bidirectional coupling of the two components that constitute prehension (cf. Hoff and Arbib 1993). Our data might be taken to show the necessity of such a step. Whereas, in accordance with the simulated results, for five of the six stationary-object conditions, the $TC_1(D)$-value at which hand closure started increased with increasing reaching amplitude, this pattern was not maintained for the 20-cm stationary-object condition, where a relatively large $TC_1(D)$-value was experimentally observed (see Fig. 6). We suggest that this change in pattern is due to an influence of the grasp component on the reach component. Perturbation experiments have indicated that, besides the influence of the reach component on the grasp component, as modeled here, the grasp component in its turn affects the reach component (Castiello et al. 1993; Paulignan et al. 1991a). The latter effect was not incorporated in the present model and may be expected to manifest itself most clearly in the situation in which movement amplitude is relatively small (cf. Hoff and Arbib 1993). Further modeling of the grasp component's dynamics, necessary for the extension of the present model, could proceed from the observation that speed-amplitude relations in the grasp component resemble those observed in the reach component (Bootsma et al. 1994; Zaal and Bootsma 1993).

Before drawing this paper to a close, we would like to emphasize once more that the coordination of the reaching and grasping component has been analyzed here at the behavioral level. With respect to the neural structures involved in the control of prehension, a significant body of evidence suggests that two parallel neural processes underlie reaching and grasping (Jeannerod 1988; Soechting and Flanders 1993). In macaque monkeys, premotor area F5 has been reported to express grasping-related activity (Jeannerod et al. 1995; Rizzolatti et al. 1988). Rizzolatti et al. (1996), on the other hand, reported that not all neuronal activity observed in the monkey could be mapped onto activity in functionally similar structures in humans, adding that this might be due to differences in specific aspects of the tasks the monkeys and the humans performed. On the basis of a study of the regional cerebral blood flow during reaching and grasping, Matsumara et al. (1996) recently suggested that the bilateral premotor area, the posterior parietal area, and the prefrontal area may be key structures involved in grasping as compared to reaching. Van Kan et al. (1994) demonstrated that high discharge modulation of interpositus neurons in monkeys distinguished between reaching to grasp relative to reaching per se. Findings like these provide a neurophysiological underpinning of the functional separation of reaching and grasping. A next step might be the search for collective phenomena of brain activity that are related to aspects of the coordination of reaching and grasping as described in our model. Until now reaching and grasping has been understood as controlled by more microscopic aspects of brain activity. However, since there are no compelling reasons to favor the latter level over macrostates (Kelso 1995), we suggest that the relation between the behavioral aspects of the coordination of reaching and grasping and collective brain states in terms of common dynamics should be pursued. The present article may be considered as a necessary, albeit not sufficient, step in preparing the ground for such an investigation.

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